Genetic structure of four geographic populations of *Locusta migratoria manilensis* in China

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Abstract: The genetic structure of the four geographic populations of the Oriental migratory locust *Locusta migratoria manilensis* was analyzed using horizontal starch gel electrophoresis. Among 20 loci of 13 isozymes identified, the higher the percentage of polymorphic loci ($P = 70\% - 80\%$), the lower the observed overall heterozygosity ($H_o = 0.023 - 0.032$). The result from Chi-square test for the genotype frequencies showed the genotype frequency at most loci deviated significantly from Hardy-Weinberg equilibrium except *Adk*-1, *Gdh*-1, *G3pd*-1 and *Pgm*-1. Based on *F*-statistics (average $F_{st} = 0.0606$), an extremely small genetic differentiation among the four populations was observed. It appeared that the long-distance migration of the locust enhanced gene flow and decreased genetic differentiation. The divergence among four populations was revealed using Nei's genetic identity (I) and Roger's genetic distance (D). The higher the genetic identity, the smaller the genetic distance observed between Shanxi-Linyi and Shanxi-Yongji populations ($I = 0.964$, $D = 0.175$), and between Jiangsu-Peixian and Henan-Zhongmou populations ($I = 0.957$, $D = 0.160$). The results indicated that there was a positive relationship between genetic differentiation and geographic distance.

Key words: *Locusta migratoria manilensis*; population; genetic differentiation; allozyme; China

Allozyme analysis has been extensively applied to population genetics and systematics. It can examine a large number of individuals at many loci, and could be used as the first step to examine population genetic structure and differentiation (Richardson *et al.*, 1986; Murphy *et al.*, 1990).

The researches on the taxonomy, morphology, anatomy and physiology, the change of occupancy areas and the plague occurrence of *Locusta migratoria* had been well documented (Chen, 2000a). In recent years, the studies on it had focused on ecology, biochemistry and especially molecular systematics (Li and Ma, 2003), and its mtDNA sequencing had been completed (Flook *et al.*, 1995). However, the population genetic structure of locust species using the allozyme data was very scarcely studied before 2000 (Moran *et al.*, 1980; Daly *et al.*, 1981; Chapco and Bidochka, 1986), and only in recent years several related studies were reported in China (Han *et al.*, 2002; Qiao *et al.*, 2002; Zheng *et al.*, 2002; Li *et al.*, 2003).

Locusta migratoria L. (Orthoptera: Acridoidae) is one of the most serious agricultural pests. The locust has ten subspecies. In China, three subspecies have been documented: *Locusta migratoria manilensis* (Meyen), *L. migratoria migratoria* (Linnaeus) and *L. migratoria tibetensis* Chen. The Oriental migratory locust, *L. migratoria manilensis* is the most common subspecies, and distributed in Southeast Asia including Philippines, Thailand, Cambodia, Japan, China and so on (Zhu, 1999). There are five basic types of locust breeding areas in Asia (especially in China): the lakeshore locust area, the river flood locust area, the seacoast locust area, the inland plain flood area and the tropical savanna grassland locust breeding area (Ding, 1995; Liu, 1995). In habitability, *L. migratoria manilensis* is classified into two morphologically different categories: the solitary phase and the gregarious phase. However, the intermediate phases or transient phases are found frequently (Chen, 1999).

Here we studied the genetic variability of the locust populations in China and the genetic differentiation among the four populations, and analyzed the factors affecting the genetic differentiation of populations.

1 MATERIALS AND METHODS

1.1 Materials

Four population samples of *L. migratoria manilensis* were collected from Jiangsu, Henan and Shanxi in China between July and September in 2001.

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The collection data are listed in Table 1. The samples were brought to the laboratory alive, marked and frozen at −80℃ until used for electrophoresis.

Thirteen isozymes were identified: AAT, ADK, AO, EST, FBP, GDH, G3PD, IDH, LDH, MDH, ME, PGI and PGM.

Starch gel (12.5%) was prepared with the mixture of soluble starch, potato starch (Sigma S-5651) and refined starch (self-prepared) at a ratio of 2∶1∶1. The enzymes, gel buffers and other electrode conditions are listed in Table 2. For all buffers, the concentration ratio of electrode to gel buffer is 9∶1.

Table 1 The collecting sites of four populations of *Locusta migratoria manilensis* in China

Population	Collecting site	Locust area type	Location	Individuals collected
Jiangsu-Peixian	Peixian, Jiangsu	Lakeshore	E 116°4′ N 38°4′	202
Henan-Zhongmou	Zhongmou, Henan	River flood	E 114° N 34°73′	198
Shanxi-Linyi	Linyi, Shanxi	River flood	E 110°7′ N 35°21′	192
Shanxi-Yongji	Yongji, Shanxi	Inland plain flood	E 110°38′ N 35°1′	178

Table 2 Enzyme systems and electrophoretic conditions used in allozyme analysis

Code	Enzyme	E.C.No.	Buffer*	Voltage (V)	Duration (h)
AAT	Aspartate aminotransferase	2.6.1.1	TEM	220	4.5
ADK	Adenylate kinase	2.7.4.3	Pi	250	5.5
AO	Aldehyde oxidase	1.2.3.1	Pi	250	5.5
EST	Esterase	3.1.1.-	Pi	250	5.5
FBP	Fructose-bisphosphate aldolase	3.1.3.11	TEM	220	4.5
GDH	Glutamate dehydrogenase	1.4.1.2	TEM	220	4.5
G3PD	Glyceraldehyde-3-phosphase dehydrogenase	1.2.1.12	Pi	250	5.5
IDH	Isocitrate dehydrogenase	1.1.1.42	TCA	220	5.0
LDH	Lactate dehydrogenase	1.1.1.27	TCA	220	5.0
MDH	Malate dehydrogenase	1.1.1.37	Pi	250	5.5
ME	Malic enzyme	1.1.1.40	TCA	220	5.0
PGI	Phosphoglucoisomerase	5.3.1.9	Pi	250	5.5
PGM	Phosphoglucomutase	5.4.2.2	Pi	250	5.5

* TEM: 0.1 mol/L Tris-EDTA-Malate-$MgCl_2$, pH 7.6; Pi: 0.05 mol/L phosphate buffer, pH 8.0; TCA: 0.1 mol/L Tris-Citric-Acid, pH 8.0.

1.2 Methods

Femur muscle tissue was removed from the locust and homogenized in 20 μL double distilled water on an ice pan. Filter papers (3 mm × 9 mm) were used as wicks for loading samples. The size of the gel mold was 235 mm × 135 mm × 8 mm. Electrophoresis was conducted at 4℃ refrigerator with constant voltage (Table 2).

After electrophoresis, the gel was sliced horizontally into three pieces: each was used to stain for one kind of enzyme activity using a specific substrate. Allozyme staining was conducted according to the standard methods (Richardson *et al*., 1986; Murphy *et al*., 1990; Wang, 1998) with modifications. In zymogram scoring, alleles were identified from anode to cathode by labeling the fastest migrating allele as "A", the second fastest allele as "B", and so on.

The software BIOSYS-Ⅱ (Swofford and Selander, 1981) was used to calculate allele frequency, goodness-of-fit for Hardy-Weinberg equilibrium, the percentage of polymorphic loci (P), the mean number of alleles per locus (A), mean heterozygosity (H), F-statistics (F_{st}), Nei's genetic identity (I) and Roger's genetic distance (D). The cluster analysis based on the Nei's genetic identity (I) and Roger's genetic distance (D) was conducted using unweighted pair-group method with arithmetic averaging (UPGMA) (Richardson *et al*., 1986).

2 RESULTS

2.1 Zymogram

The 13 enzymes (Table 2) revealed 20 scorable loci with consistent clear bands and sufficient resolution. Four enzymes, ADK, G3PD, PGI and PGM, presented different subbands due to the

experiment condition. The result of electrophoresis showed that most of stained enzymes migrated from cathode to anode except three enzymes (*Aat*-2, *Gdh*-2 and *Mdh*-2). In addition, no distinct difference in allozyme character was observed between the males and females, but obvious difference in enzyme activity was found between the nymphs and the adults.

2.2 Allele frequency

In the four populations, there were 16 polymorphic loci with 61 alleles. Six enzymes, AAT, AO, GDH, IDH, LDH and MDH, revealed two loci. However, three loci were observed in EST (Table 3). Of the 21 loci, the *Idh*-2 locus could not be scored, as the bands stained were very weak and unstable.

Table 3 Allele frequencies and Chi-square test for Hardy-Weinberg's expectation of genotype frequencies in the four populations of *Locusta migratoria manilensis*

Locus	Population	*n*	Allele frequency				χ^2
			A	B	C	D	
Aat-1	Jiangsu-Peixian	45	0.667	0.311	0.022	0.000	53.00
	Henan-Zhongmou	45	0.660	0.356	0.044	0.000	58.80*
	Shanxi-Linyi	45	0.440	0.600	0.000	0.000	46.02*
	Shanxi-Yongji	45	0.660	0.378	0.022	0.000	52.44*
Aat-2	Jiangsu-Peixian	45	0.378	0.600	0.022	0.000	43.57*
	Henan-Zhongmou	45	0.578	0.422	0.000	0.000	38.10*
	Shanxi-Linyi	45	0.067	0.844	0.089	0.000	53.95*
	Shanxi-Yongji	45	0.222	0.700	0.078	0.000	64.25*
Adk-1	Jiangsu-Peixian	74	0.986	0.014	0.000	0.000	75.00*
	Henan-Zhongmou	55	0.991	0.009	0.000	0.000	0.00
	Shanxi-Linyi	37	1.000	0.000	0.000	0.000	
	Shanxi-Yongji	30	1.000	0.000	0.000	0.000	
Ao-1	Jiangsu-Peixian	45	0.667	0.311	0.022	0.000	191.66*
	Henan-Zhongmou	45	0.660	0.356	0.044	0.000	126.51*
	Shanxi-Linyi	45	0.440	0.600	0.000	0.000	85.83*
	Shanxi-Yongji	45	0.660	0.378	0.022	0.000	181.85*
Ao-2	Jiangsu-Peixian	119	0.983	0.017	0.000	0.000	120.01*
	Henan-Zhongmou	115	0.623	0.370	0.017	0.000	111.17*
	Shanxi-Linyi	66	0.629	0.364	0.008	0.000	53.53*
	Shanxi-Yongji	45	0.467	0.356	0.178	0.000	84.32*
Est-1	Jiangsu-Peixian	70	0.336	0.364	0.300	0.000	92.41*
	Henan-Zhongmou	45	0.378	0.489	0.133	0.000	56.81*
	Shanxi-Linyi	41	0.402	0.244	0.354	0.000	76.09*
	Shanxi-Yongji	63	0.063	0.635	0.222	0.079	130.36*
Est-2	Jiangsu-Peixian	83	0.602	0.392	0.006	0.000	78.77*
	Henan-Zhongmou	55	0.545	0.400	0.055	0.000	74.22*
	Shanxi-Linyi	51	0.863	0.137	0.000	0.000	52.01*
	Shanxi-Yongji	66	0.735	0.258	0.008	0.000	65.63*
Est-3	Jiangsu-Peixian	43	0.302	0.488	0.174	0.035	68.00*
	Henan-Zhongmou	55	0.236	0.291	0.345	0.127	132.30*
	Shanxi-Linyi	51	0.314	0.490	0.118	0.078	115.12*
	Shanxi-Yongji	66	0.265	0.379	0.295	0.061	99.67*
Fbp-1	Jiangsu-Peixian	45	0.662	0.333	0.044	0.000	59.11*
	Henan-Zhongmou	45	0.711	0.267	0.022	0.000	43.03*
	Shanxi-Linyi	45	0.844	0.111	0.044	0.000	69.38*
	Shanxi-Yongji	45	0.589	0.411	0.000	0.000	41.93*
Gdh-1	Jiangsu-Peixian	45	0.978	0.022	0.000	0.000	46.02*
	Henan-Zhongmou	45	0.989	0.011	0.000	0.000	0.00
	Shanxi-Linyi	45	0.978	0.022	0.000	0.000	46.02*
	Shanxi-Yongji	45	1.000	0.000	0.000	0.000	
Gdh-2	Jiangsu-Peixian	45	0.778	0.200	0.022	0.000	55.11*
	Henan-Zhongmou	45	0.533	0.467	0.000	0.000	46.02*
	Shanxi-Linyi	45	0.644	0.289	0.067	0.000	65.90*
	Shanxi-Yongji	45	0.822	0.178	0.000	0.000	46.02*

Table 3 (continued)

Locus	Population	*n*	Allele frequency				χ^2
			A	B	C	D	
G3pd-1	Jiangsu-Peixian	74	0.000	1.000	0.000	0.000	
	Henan-Zhongmou	113	0.004	0.996	0.000	0.000	0.00
	Shanxi-Linyi	142	0.000	1.000	0.000	0.000	
	Shanxi-Yongji	50	0.000	1.000	0.000	0.000	
Idh-1	Jiangsu-Peixian	75	0.167	0.740	0.093	0.000	103.51*
	Henan-Zhongmou	88	0.080	0.784	0.136	0.000	112.18*
	Shanxi-Linyi	114	0.311	0.513	0.175	0.000	192.78*
	Shanxi-Yongji	72	0.257	0.688	0.056	0.000	95.45*
Ldh-1	Jiangsu-Peixian	139	0.723	0.209	0.068	0.000	190.26*
	Henan-Zhongmou	128	0.516	0.477	0.008	0.000	118.98*
	Shanxi-Linyi	103	0.568	0.413	0.019	0.000	103.45*
	Shanxi-Yongji	98	0.577	0.403	0.020	0.000	98.41*
Ldh-2	Jiangsu-Peixian	45	1.000	0.000	0.000	0.000	
	Henan-Zhongmou	57	0.860	0.140	0.000	0.000	58.01*
	Shanxi-Linyi	103	0.791	0.209	0.000	0.000	98.01*
	Shanxi-Yongji	81	0.944	0.056	0.000	0.000	63.95*
Mdh-1	Jiangsu-Peixian	139	0.284	0.716	0.000	0.000	125.60*
	Henan-Zhongmou	147	0.122	0.878	0.000	0.000	97.28*
	Shanxi-Linyi	83	0.090	0.910	0.000	0.000	72.22*
	Shanxi-Yongji	84	0.101	0.899	0.000	0.000	74.31*
Mdh-2	Jiangsu-Peixian	119	0.908	0.092	0.000	0.000	120.01*
	Henan-Zhongmou	147	0.690	0.238	0.068	0.003	210.09*
	Shanxi-Linyi	83	0.608	0.295	0.096	0.000	126.44*
	Shanxi-Yongji	84	0.899	0.095	0.006	0.000	70.92*
Me-1	Jiangsu-Peixian	129	0.748	0.213	0.039	0.000	164.32*
	Henan-Zhongmou	188	0.612	0.367	0.019	0.003	183.55*
	Shanxi-Linyi	85	0.353	0.535	0.112	0.000	112.24*
	Shanxi-Yongji	147	0.401	0.490	0.100	0.000	204.28*
Pgi-1	Jiangsu-Peixian	113	0.168	0.456	0.332	0.044	183.86*
	Henan-Zhongmou	138	0.243	0.420	0.264	0.072	255.95*
	Shanxi-Linyi	121	0.314	0.379	0.240	0.050	238.12*
	Shanxi-Yongji	100	0.230	0.450	0.270	0.050	168.96*
Pgm-1	Jiangsu-Peixian	85	1.000	0.000	0.000	0.000	
	Henan-Zhongmou	113	0.996	0.004	0.000	0.000	0.00
	Shanxi-Linyi	60	1.000	0.000	0.000	0.000	
	Shanxi-Yongji	50	1.000	0.000	0.000	0.000	

* Significantly different from Hdy-Wbg expectations ($P < 0.01$, Chi-square with pooling was used).
n: Individual number used at each locus; A, B, C, and D: Allele at a locus.

Six loci (*Adk*-1, *Pgm*-1, *Ldh*-2, *Gdh*-1, *G3pd*-1 and *Mdh*-1) demonstrated lower variability, whereas loci like *Est*-1, *Est*-3 and *Pgi*-1 were highly variable with at least two alleles.

2.3 Genetic variability

Among the 20 loci examined, *Adk*-1 in Jiangsu-Peixian population and *Gdh*-1 in Shanxi-Yongji population were polymorphic. *G3pd*-1 and *Pgm*-1 were monmorphic loci across all the four populations according to criterion 2 (95%).

Genotype frequencies deviated remarkably from the Hardy-Weinberg's expectations at most loci. Four loci, *Adk*-1, *Gdh*-1, *G3pd*-1 and *Pgm*-1, were found to fit to the Hardy-Weinberg's predictions, but the all four loci appeared in Henan-Zhongmou population (Table 3).

All four populations demonstrated high percentage of polymorphic loci and low observed overall heterozygosity. However, the percentage of polymorphic loci in Jiangsu-Peixian population is notably lower than that in the rest three populations (Table 4).

Table 4 Genetic variability of the four populations of *Locusta migratoria manilensis*

Population	Mean sample size per locus	Mean number of alleles per locus (*A*)	Percentage of polymorphic loci (*P*)*	Mean heterozygosity	
				Direct-count (H_o)	Hdy-Wbg expection**
Jiangsu-Peixian	82.8 (8.0)	2.6 (0.2)	70.0%	0.026 (0.009)	0.339 (0.054)
Henan-Zhongmou	89.2 (10.1)	2.8 (0.2)	80.0%	0.032(0.006)	0.392 (0.051)
Shanxi-Linyi	71.9 (6.9)	2.5 (0.2)	80.0%	0.023(0.007)	0.381 (0.054)
Shanxi-Yongji	67.8 (6.3)	2.6 (0.2)	80.0%	0.026(0.009)	0.369 (0.056)

* A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95. ** Unbiased estimate (Nei, 1978).

2.4 F-statistics

F-statistics was used for analyzing the genetic differentiation among populations. The average F_{is} values was relatively high ($F_{is} = 0.9262$) but average F_{st} was very low ($F_{st} = 0.0606$), which reflected the high genetic variation within population and the low genetic differentiation among populations.

2.5 Nei's genetic identity and Roger's genetic distance

Nei's genetic identity (I) and Roger's genetic distance (D) showed the divergence among four populations: the higher the genetic identity, the smaller the genetic distance observed between Shanxi-Linyi and Shanxi-Yongji populations ($I = 0.964$, $D = 0.175$), and between Jiangsu-Peixian and Henan-Zhongmou populations ($I = 0.957$, $D = 0.160$). There were lower genetic identity and bigger genetic distance between the former two populations and the later two populations (Table 5, Figs. 1 and 2).

Table 5 Nei(1978)genetic identity(I)and Roger(1978) genetic distance(D) among four populations of *L. m. manilensis* (Upper diagonal: D; lower diagonal: I)

Population	Jiangsu-Peixian	Henan-Zhongmou	Shanxi-Linyi	Shanxi-Yongji
Jiangsu-Peixian		0.175	0.200	0.164
Henan-Zhongmou	0.957		0.195	0.166
Shanxi-Linyi	0.942	0.943		0.160
Shanxi-Yongji	0.963	0.960	0.964	

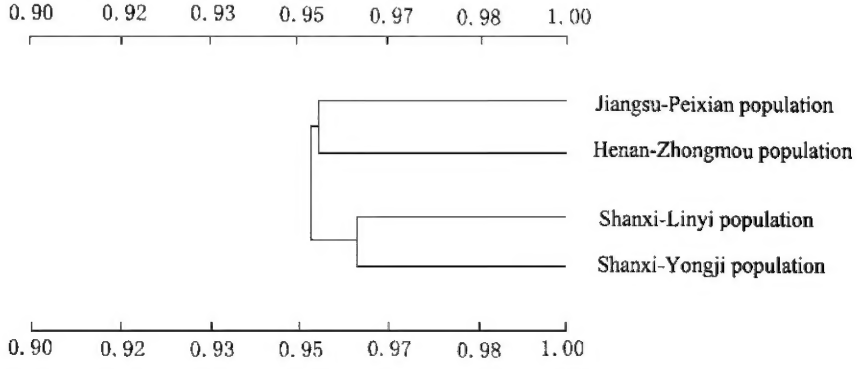

Fig.1 Cluster analysis based on Nei's genetic identity in the four populations of *Locusta migratoria manilensis*

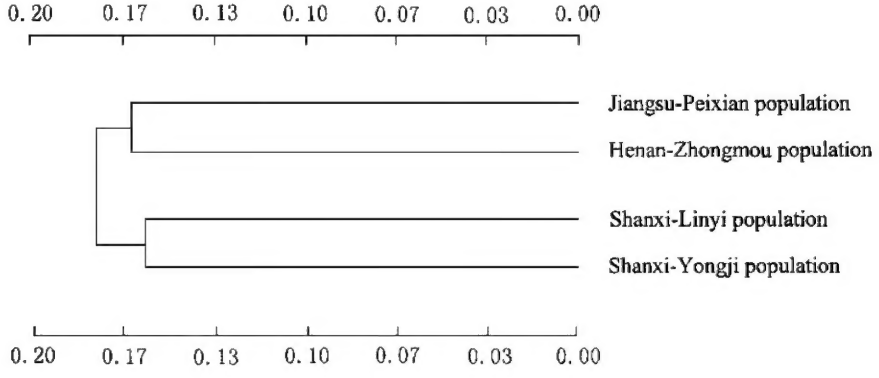

Fig.2 Cluster analysis based on Roger's genetic distance in the four populations of *Locusta migratoria manilensis*

3 DISCUSSION

The migratory feature of *L. migratoria manilensis* could be served as a mechanism to maintain the genetic composition at population level. The genetic polymorphism within population may depend on at least two factors that are all related to migration. Firstly, the unusual dispersal capability of the locust tends to make a continuous genetic structure distribution. Secondly, the frequent migration could make the individuals to be exposed to various environments, which calls for the maintenance of higher genetic polymorphism. It has been found that the genetic variability of *L. migratoria manilensis* (Table 4) is notably higher than the other migratory grasshoppers studied, such as the grasshopper *Melanoplus sanguinipes* ($P = 37.8\%$) (Chapco and Bidochka, 1986).

The considerably low mean heterozygosity was observed in the four populations of *L. migratoria manilensis* (Table 4), which might be related to the three abiotic and biotic factors. Firstly, gregarious

effect and behavior could cause close breeding habit. Secondly, parthenogenesis has been reported in *L. migratoria manilensis* (Guo, 1956). A special reproductive behavior as such could make the homozygotes increased and heterozygotes decreased. Thirdly, the bottleneck effect was often occurred in the four locust areas owing to the large-scale application of insecticides. The above factors also made the most loci of the four populations deviated significantly from Hardy-Weinberg equilibrium, and some additional factors, such as gene flow, inbreeding, null alleles, population subdivision, natural selection and frequent migration, might also contribute to this deviation.

L. migratoria manilensis has extraordinary migratory capability. It has been recorded that the swarms of the locust flew 50 km from Beidagang, Tianjin to merge with the local populations in Huanghua, Hebei Province in 1985 (Chen, 2000b). The long-distance and a large scale of migration enhanced gene flow, which made the genetic differentiation decreased. In addition, *L. migratoria manilensis* has powerful gregarious feature. Large populations also could reduce the speed with which populations differentiate from each other through genetic drift (Xin *et al.*, 2000). The extremely low F_{st} values testified the low genetic differentiation among populations ($F_{st} = 0.0606$).

The genetic differentiation among populations was greatly influenced by geographic distance (G) that is related to the migration of *L. migratoria manilensis*. A positive relationship between genetic differentiation and geographic distance was found (Figs.1 and 2) based on Nei's genetic identity (I) and Roger's genetic distance (D). The higher the genetic identity, the smaller the genetic distance observed between Shanxi-Linyi and Shanxi-Yongji populations ($D = 0.160$, $I = 0.964$, $G = 48$ km), and between Jiangsu-Peixian and Henan-Zhongmou populations ($D = 0.175$, $I = 0.957$, $G = 258$ km). Some probable causes could account for the phenomenon. Firstly, the long-distance migration leads to gene flow among populations, which might decrease genetic diversity. Secondly, the samples of *L. migratoria manilensis* were collected from the four locust areas of different geographic positions (Table 1). Differences of other geographic and environment factors, such as divergent altitudes, longitude, relative humidity and so on, also had effects on the genetic differentiation.

Further studies are necessary to clarify the genetic background of *L. migratoria manilensis* by analyzing more populations at most loci. In addition, genetic differentiation among populations was affected by locust's migratory capability that is closely related to gregarious character. It is also necessary to probe into the genetic difference between solitary phase and gregarious phase in this locust.

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中国东亚飞蝗四个地理种群遗传结构的比较研究

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摘要: 利用水平切片淀粉凝胶电泳技术, 分析了不同蝗区东亚飞蝗四个地理种群的遗传结构。在检测的 20 个酶基因座位中, 四个种群均表现出一定的遗传多态性, 多态位点的百分率普遍偏高 ($P = 70\% \sim 80\%$), 但由于杂合子数目较少而使每个位点的平均杂合度观察值偏低 ($H_o = 0.023 \sim 0.032$)。对每个基因座位的各基因型进行 χ^2 检验, 除 *Adk*-1、*Gdh*-1、*G3pd*-1 和 *Pgm*-1 在部分种群符合 Hardy-Weinberg 平衡外, 其余绝大多数基因座位的基因型频率显著偏离 Hardy-Weinberg 平衡。从 F 统计量看, 四个种群之间的遗传分化较低 ($F_{st} = 0.0606$)。它表明: 东亚飞蝗较强的长距离迁飞行为增加了种群之间的基因交流, 降低了种群之间的遗传分化。根据 Nei 的遗传一致度 (I) 和 Roger 的遗传距离 (D) 进行分析, 在山西临猗与山西永济 ($I = 0.964$, $D = 0.175$)、河南中牟与江苏沛县种群 ($I = 0.957$, $D = 0.160$) 之间, 呈现出较高的遗传一致度和较小的遗传距离。结果表明: 迁飞性蝗虫东亚飞蝗种群之间的遗传分化与地理距离呈正相关。

关键词: 东亚飞蝗; 种群; 遗传分化; 等位酶; 中国
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